

**On Brinkmann's System of the Nemertea
Enopla and Siboganemertes Weberi, n.g.n.sp.**

By

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With 26 Text-figures.

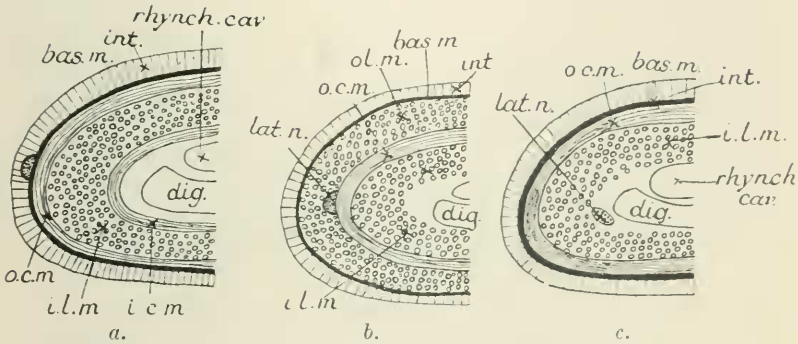
ALL text-books of zoology give the Nemertean system as Bürger published it several times in his monographs on this subject (6, 7, 8). The old systems of Schultze, McIntosh, Hubrecht have been forsaken, and our text-books do not divide the Nemertini any more in Anopla and Enopla, or Palaeonemertea, Hoplonemertea, and Schizonemertea. The armature of the proboscis and the arrangement of the cephalic slits are believed to be of secondary importance, and Bürger divided the Nemertini into four orders, three of which, his Protonemertini, Mesonemertini, and Metanemertini are supposed to be closely related by having a body-wall that consists of an epithelium, a basement membrane, and two muscular layers. Benham, in Ray Lankester's 'Treatise on Zoology', unites them as Dimyaria, and his Trimyaria consist of one order only, the Heteronemertini Bürger. The Protonemertini are McIntosh's family Carinellidae, Mesonemertini are his family Cephalotricidae and the genus Carinoma (Hubrecht); Metanemertini is a new name for Hoplonemertini (Hubrecht) or Enopla (Max Schultze), and Heteronemertini are Hubrecht's Schizonemertini and his families Eupoliidae and Valenciidae. Everybody agrees that the last two families are more nearly related to Lineids and Cerebratulids than to the Protonemerteans, and their enclosure in the order Heteronemertini seems to be well

founded. The following schema gives the synonyms in the different systems.

Max Schultze.	McIntosh.	Hubrecht.	Bürger.	Blaxland Benham.
Enopla	fam. Amphiporidae fam. Cephalothricidae	Hoploneimertini. fam. Cephalothricidae gen. Carinoma fam. Carinellidae	Meta- nemertini	} Dimyaria.
Anopla	fam. Carinellidae fam. Lineidae	fam. Eupoliidae fam. Valencinellidae Schizonemertini	Meso- nemertini Proto- nemertini	
			Hetero- nemertini	
			Palaeo- nemertini	

The combination of Bürger's three other orders in the Dimyaria was not well founded. Bürger meant them to be two stages in the development of the third, the Metanemerteans or Hoplonemertini; the Protonemertini with their epithelial nervous system (Text-fig. 1, *a*) being the most primitive ones. Carinoma and Cephalothrix, the Mesonemertini, give the development that leads to the central position of this system in the body parenchyma (Text-fig. 1, *c*). Now Bergendal, in his treatise on *Carinoma armandi* (2), made it clear that this genus is closely related to Carinella and the Heteronemerteans (Text-fig. 1, *b*), and has no affinity at all to Cephalothrix nor to the armed Nemerteans. In another Swedish article he shows (1) that Bürger's order Mesonemertini is quite unnatural, and that both genera Cephalothrix and Carinoma are true Protonemertini; so Hubrecht's order Palaeonemertini ought to be restored. A study on Cephalothrix taught me (16) that this genus is not nearer related to the armed Nemerteans than to the unarmed, and so we get instead of Proto- and Meso-nemertini the old order of Palaeonemertini, nearly related to the Heteronemertini and without any special relation to these groups the armed Nemerteans. In 1912 (17) I proposed to return to the old division of Max Schultze. The class Nemertini is subdivided into two sub-classes: Anopla and Enopla. Each sub-class contains two orders: the Anopla with Palaeonemertini (Hubrecht) and Heteronemertini (Bürger), of which diagnoses were given and schemes are given here in Text-fig. 1, *a* and *b*; and the Enopla

TEXT-FIG. 1.

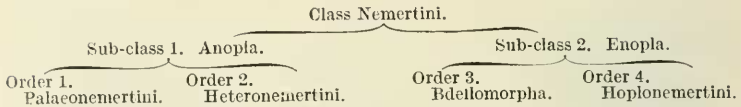


Schemata of the musculature, nervous system, and body-wall in: *a*, Palaeonemertini; *b*, Heteronemertini; *c*, Enopla. In transverse section.

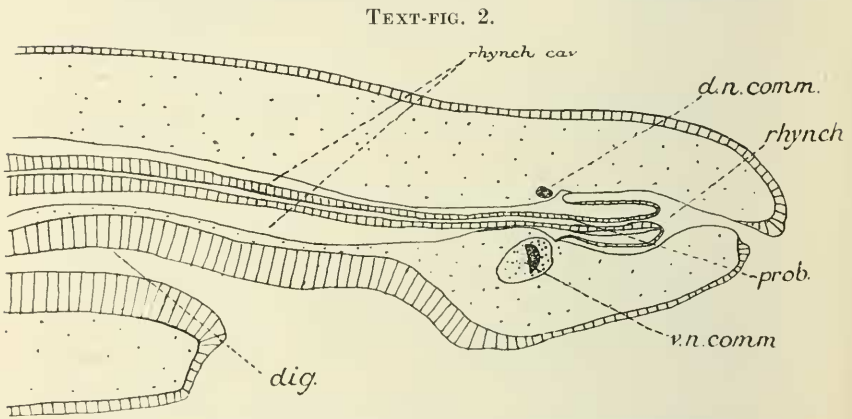
LIST OF ABBREVIATIONS.

acc.st., accessory stylet; *an.bl.v.*, unpaired anal blood-vessel; *an.l.*, anal commissure of blood-vascular system; *atr.*, atrium; *bas.*, base of stylet; *bas.m.*, basement membrane; *b.g.*, entodermal blind-gut; *bl.v.*, blood-vessel; *bod.par.*, body parenchyma; *br.*, brain; *cer.bl.c.*, cerebral blood commissure; *cer.can.*, cerebral canal; *cer.sac.*, sac of cerebral organ; *circ.m.f.*, circular muscle-fibres; *c.m.*, new circular musculature of proboscis; *d.b.v.*, dorsal blood-vessel; *d.g.*, dorsal ganglion; *dig.*, digestive tract; *d.n.comm.*, dorsal nerve commissure; *ej.d.*, ejaculatory duct; *gangl.*, ganglionic part of cerebral organ; *gastr.*, gastric cavity; *gl.*, glands; *g.p.*, gonopore; *g.s.*, gonadial sac; *i.c.m.*, inner circular muscle-coat; *i.l.m.*, inner longitudinal muscle-coat; *int.*, integument; *int.p.*, intestinal pouch; *lat.n.*, lateral nerve-cord; *l.b.v.*, lateral blood-vessel; *l.m.f.*, longitudinal muscle-fibre; *m.*, mouth; *m.bl.c.*, metamerial blood-vessel commissure; *musc.sept.*, muscular septum; *neph.*, nephridium; *o.c.m.*, outer circular musculature; *oes.*, oesophagus; *o.l.m.*, outer longitudinal musculature; *ov.*, ovary; *p.e.*, proboscidian epithelium; *p.end.*, proboscidian endothelium; *p.p.*, proboscis pore; *prob.*, proboscis; *prob.cav.*, proboscidian cavity; *prob.n.*, proboscidian nerve; *prob.w.*, proboscidian wall; *pyl.*, pylorus; *rad.m.*, dorsoventral musculature; *rh.c.m.*, normal circular coat of rhynchocoelomic wall; *rh.l.m.*, normal longitudinal coat of rhynchocoelomic wall; *rhynch.*, rhynchodaeum; *rhynch.bl.v.*, rhynchocoelomic vessel; *rhynch.cav.*, rhynchocoelomic cavity; *rhynch.div.*, rhynchocoelomic diverticula; *rhynch.end.*, rhynchocoelomic endothelium; *rhynch.m.*, rhynchocoelomic musculature; *rhynch.w.*, rhynchocoelomic wall; *sac.*, sac with accessory stylets; *st.*, stylet; *t.*, testis; *v.g.*, ventral ganglion; *v.g.s.*, V-shaped gonadial sac; *v.n.comm.*, ventral nerve commissure of the brain.

with Bdellomorpha (Verrill) and Hoplonemertini (Hubrecht) (Text-fig. 1, c).



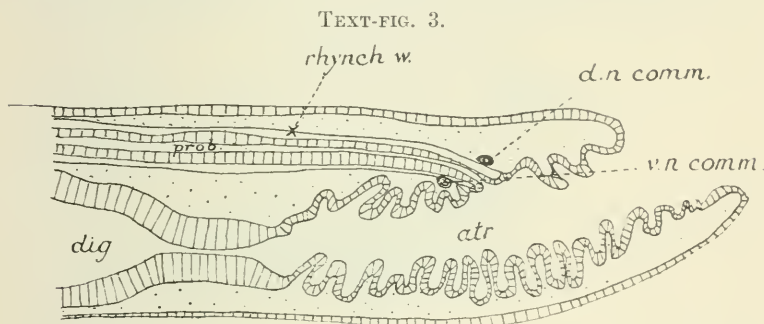
The sub-class Enopla (Text-fig. 1, c) shows a tendency to have the digestive system and the proboscidian apparatus opening to the exterior by one aperture. In the Anopla both openings



Schematic longitudinal section of an unarmed Nemertean after Bürger (6, Pl. xxi, fig. 1, *Cerebratulus marginatus*).

are always widely separated, as shown in Text-fig. 2; in the Enopla the common aperture is obtained in different ways. The Bdellomorpha, containing the parasitic genus *Malacobdella*, which Bürger included in his Metanemertini, though it lacks an armed proboscis and shows great differences in the structure of almost every organ, has its proboscis inserted in the wall of the stomodaeum (Text-fig. 3). In the Hoplonemertea the same result, one common mouth, is developed in two other ways, as will be shown afterwards. As Bürger's Metanemertini are only a newer name for Hoplonemertini his subdivision of this order into Pro- and Holo-rhynchocoelomia might be followed in our system as well. The main difference between these

sub-orders exists in the length of the proboscis sheath, which in the first group is developed in part of the body only, in the Holorhynchocoelomia, however, is present from the snout to the tail. That this division is unnatural Brinkmann showed in his monograph on the pelagic Nemerteans (4). In this most interesting paper, that contains the minute anatomical description of eighteen genera of pelagic Nemerteans with thirty-two species, the greater part of which are new, Brinkmann describes nearly related species of one genus, *Balaenanemertes*, that might be types of Bürger's

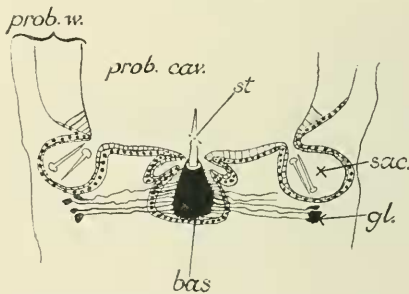


Schematic longitudinal section of *Malacobdella grossa* after Bürger (6, Pl. xviii, fig. 2).

two sub-orders. In other genera the difference is less great but still exists. This fact alone is sufficient to demonstrate the unnaturalness of the subdivision of Bürger's *Metanemertini*. Another fact of interest was that all pelagic forms are nearly related, and show a peculiarity in the armature of the proboscis that we knew only from the genus *Drepanophorus*. This genus is one of Bürger's Holorhynchocoelomia. Though at first included in the family Amphiporidae, the family *Drepanophoridae* was later established; and Bürger believed this genus with its paired rhynchocoelomic diverticula to be the most highly specialized one of his sub-class. In his study on *Uniporus*, a nearly related genus, Brinkmann (3) came to the conclusion that the *Drepanophoridae* in many respects are very primitive forms of *Hoplonemerteans*, which

conclusion I share. All these facts show evidently that Bürger's system of Metanemertini does not give the real relationship of the genera. Brinkmann gives another system, that seems to suit much better our present state of knowledge. The armature of the proboscis is the distinctive character. In most armed Nemerteans the proboscis has one stylet on the top of a somewhat pear-shaped handle (Text-fig. 4). The only known exception to this rule was till fifteen years ago *Drepanophorus*; then the *Valdivia* material showed that some of the pelagic Nemerteans have a crescent-shaped handlelike *Drepanophorus* with many small stylets (Text-fig. 5)

TEXT-FIG. 4.

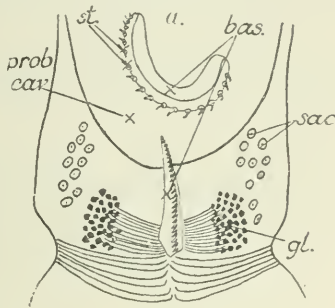


Armature of the proboscis of *Stichostemma eithardi* after Montgomery, 1894 ('Zool. Anzeiger', Jahrgang 17, fig. 3) (Monostilifera).

and Brinkmann (4) confirmed this discovery of Bürger for all pelagic forms. He divides the Hoplonemertini into two sub-orders, Polystilifera and Monostilifera (4, p. 145). The Monostilifera contain all genera of Metanemertini (Bürger), with the exception of (1) *Malacobdella* (= *Bdellomorpha*, Verrill), (2) the pelagic genera, and (3) *Drepanophoridae*. The Polystilifera consist of all pelagic Nemerteans and the genera *Drepanophorus* (Hubrecht), and *Uniporus* (Brinkmann). There can be no doubt as to the naturalness of these sub-orders. Both contain a great number of genera and species, which are widely different in structure, but still are more closely related to each other than to any other form. This is shown by the position of the mouth, which in the *Anopla* lies behind

the brain. The proboscis pore is found in front of it, as a rule at the tip of the snout (Text-fig. 2). I remarked already that in *Enopla* both structures stand in connexion with each other; in the *Bdellomorpha* the rhynchodaeum is absent and the proboscis cavity opens into the digestive tract (Text-fig. 3). In the *Hoploneimertini*, it is said, the digestive tract opens into the rhynchodaeum (Text-fig. 6). This last fact is only true as far as concerns the *Monostilifera*. That this connexion of the two systems is not primitive is shown by the embryology.

TEXT-FIG. 5.

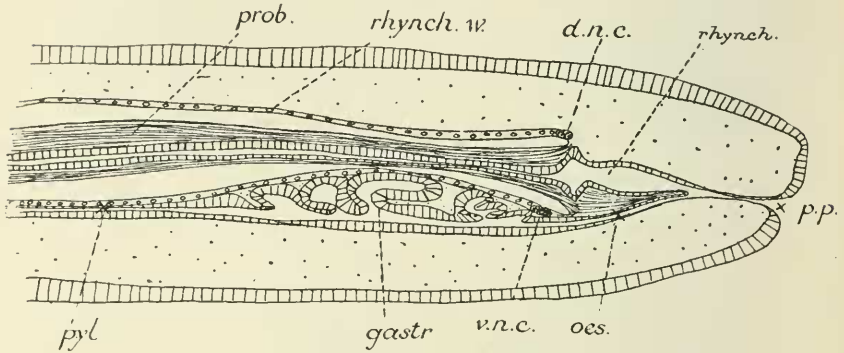


Armature of the proboscis of *Drepanophorus spectabilis* (*Polystilifera*) after Bürger (6, Pl. viii, fig. 2). *a.* Base and stylets of *D. crassus*.

In my article on the proboscidian system in Nemertines (18) I put the facts together in the following way (p. 304): 'Drepanophorus, the genus in which oesophagus and rhynchodaeum open separately, shows no connexion at all between the two systems, not even in embryology; for here the blastopore is closed, the narrow endoderm part giving rise to the blind gut by being removed forward. The primary ectodermic oesophagus invaginates near the proboscidian system, but perfectly separately. . . . In all other *Hoploneimertea* the primary oesophagus originates in exactly the same way; the mouth closes afterwards and the primary oesophagus gets a new opening to the exterior through the rhynchodaeum' (Text-fig. 7).

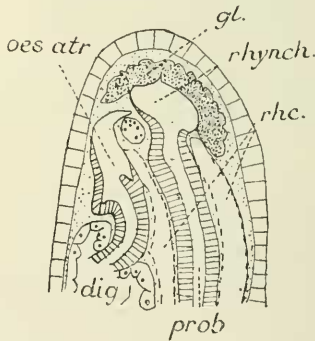
What has been said of Drepanophorus is not true for all Polystilifera. We know species in which mouth and proboscis pore are widely separated and the mouth even lies under the

TEXT-FIG. 6.



Schematic longitudinal section of a Monostilifer after Bürger (6, Pl. xv, fig. 1, *Nemertopsis peronea*).

TEXT-FIG. 7.

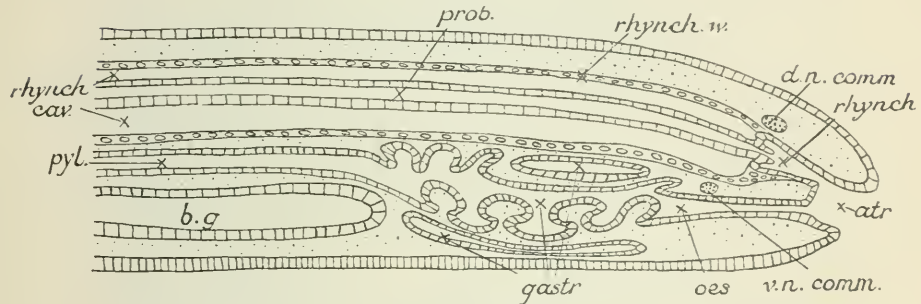


Longitudinal section through *Prosorochmus* after Salensky ("Über die embryonale Entwicklung des *P. viviparus*," 'Bull. Acad. Imp. Sciences', Petersb., 1909, fig. 8).

brain. But we also know species in which they communicate by one pore; we even know all the stages between these extremes in the Polystilifera. Brinkmann (4) showed the development of an ectodermal atrium, in which rhynchodaeum and mouth open separately in the Pelagica. He also describes

(3) a large ectodermal atrium in Uniporus, one of his Reptantia ; Drepanophorus lankesteri (Text-fig. 8) exhibits the same feature, and so do some genera of the East Indian archipelago. In the Drepanophorus species of the Channel, known as *D. spectabilis*, these openings lie quite near to each other—I might say, they touch each other ; the species known under the same name from Naples has a large space between the two, but never does the mouth open into the rhynchodaeum, nor vice versa. So there is another distinctive character between Poly- and Mono-stilifera. A difference in habits and

TEXT-FIG. 8.



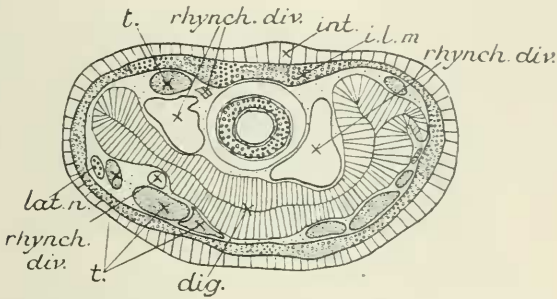
Schematic longitudinal section of *Drepanophorus lankesteri*
from sections.

manner of life accompanies the great differences of structure in Brinkmann's divisions of the Polystilifera. The Pelagica are free-swimming or hovering pelagic Nemertean that live at a great depth, without eyes, without the, for Nemertean, so characteristic cerebral organs, without a nephridial system, without rhynchocoelomic diverticula, without metamerical vascular communications. They might be considered related to the Monostilifera as well as to the Polystilifera with all these negative characters if we had not known the structure of the proboscis armature and of its sheath. Another positive character is the place of the male gonads. Though the ova develop in metamerically placed sacs between each pair of intestinal diverticula, the sperm-cells

develop only in front of this region, at the side of or directly behind the brain, a unique fact in Nemerteans. The Reptantia, containing the genera *Drepanophorus* and *Uniporus*, and, as the Siboga material shows, quite a number of other genera, that crawl about at the bottom of the sea and its coasts, have as a rule eyes and metamerial blood-vessels, but always they possess cerebral organs, nephridia, rhynchocoelomic diverticula, and metamerially placed ♂ gonads. Especially the cerebral organs are different from those of the Monostilifera and the development of a sac in this organ as well as the presence of diverticula of the proboscis sheath show that the Reptantia are widely different from the Monostilifera. Almost all Polystilifera that the Siboga expedition brought home belong to the Reptantia. About one form only there can be any doubt, as it is collected by the deep-sea trawl to the south of Timor at a depth of 883 metres. This is the depth in which most pelagic forms occur and, as occasionally pelagic Nemerteans can and have been caught by the trawl, we might be in doubt as to the manner of life of this Nemertean. Moreover the inner structure of *Siboganeustes weberi* reveals such peculiarities that we cannot with certainty decide anything. It has no eyes, but *Uniporus*, a genus of Reptantia of the Norwegian sea, living in the dis- and aphotic regions, lacks them as well. It possesses cerebral organs, but they are quite minute and of a much more primitive structure than anything known. Nephridia are present, but metamerial blood-vessels fail as in Polystilifera and *Uniporus*. Rhynchocoelomic diverticula are present, but instead of lying peripherically at the outside of all organs as in all Reptantia (Text-fig. 10) they lie inside between the proboscis sheath and the digestive tract (Text-fig. 9). The testes are placed metamerially, but they display features that we do not know in other Polystilifera. The mouth lies under the brain, which in its structure shows a great resemblance to the Pelagica and differs greatly from the Reptantia. The digestive tract, which lacks an oesophagus in the pelagic forms and has a well-developed one in the Reptantia, has quite a short balloon-like

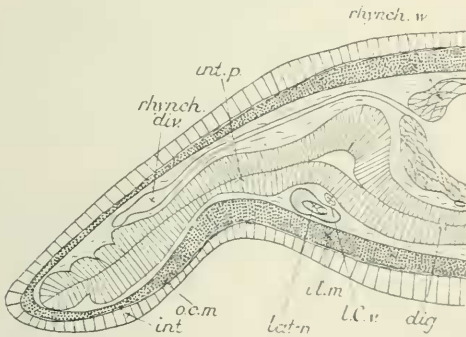
oesophagus that does not reach the brain ; on the other hand it differs greatly from that in both groups, as the different parts of the stomodaeum, that as a rule gradually pass into each other (Text-fig. 6), are sharply separated. The narrow

TEXT-FIG. 9.



Section through *Siboganemertes weberi*, n. gen. n. sp.

TEXT-FIG. 10.



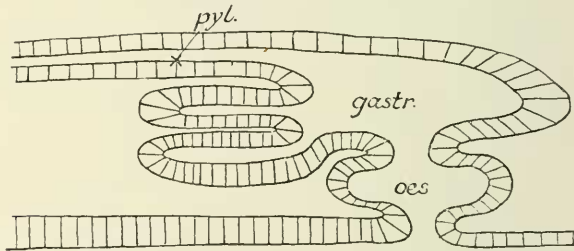
Section through *Drepanophorus albolineatus* after Bürger (6, Pl. xvii, fig. 10).

pylorus opens by a hole in the wall of the gastric cavity ; oesophagus and gastric cavity communicate by a narrow opening (Text-fig. 11). It seems evident that, though the presence of rhynchocoelomic diverticula, cerebral organs, and metamericly placed genital organs might suggest the enclosure of *Siboganemertes weberi* in the Reptantia, the

structure of the digestive system and the arrangement of the diverticula of the proboscis sheath separate them.

The most interesting feature seems to be the structure of the cerebral organ that is so highly developed in the Reptantia. This sense organ consists in the Monostilifera (Text-fig. 12, *a*) of three different parts: a channel, a ganglion, and glands. These are joined together to a more or less rounded organ with its own neurilemma. In the Reptantia the same constituents are present, but as a rule the different parts are more free from each other and partly lie outside the rounded circumference of the organ, as in *Drepanophorus cerinus* and wil-

TEXT-FIG. 11.



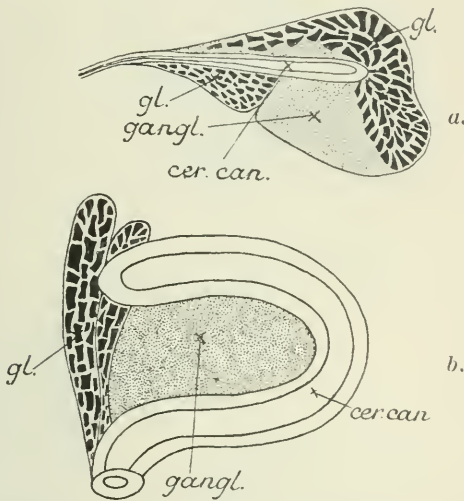
Schematic longitudinal section of the digestive tract of *Siboganeurtes weberi* after transverse sections.

leyanus (14, 15) and in *Uniporus* (3). Moreover, the duct that leads from the cephalic furrows into the cerebral organ bifurcates in the organ; one part gives rise to a more or less spacious sac, characteristic of Reptantia, and the other part ends as a narrow duct in the glandular portion of the organ (Text-fig 13). Both sac and glandular tube can lie embedded in the body parenchyma. In *Siboganeurtes* there is no bifurcation of the cerebral canal (Text-fig. 12, *b*). When the channel gets to the ganglion two small bunches of glands open into it which lie quite free. The epithelium is sensory and never gets glandular. The channel is as primitive as possible; it turns backward at the contact with the ganglion and at its end bends upward and forward on its first part, where it ends blindly. This is the most primitive cerebral

organ we know in Enopla, and makes it very probable that we stand near the origin of this organ.

As to the brain it displays very primitive features too. Brinkmann writes in his monograph (4, p. 165): 'Die den meisten Drepanophoriden so charakteristische starke Vergrößerung der dorsalen Gehirnganglien, die dazu führt, dass sie

TEXT-FIG. 12.

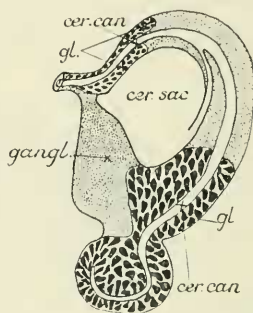


Cerebral organs of *a*, *Prostoma cephalophorum* after Bürger (6, Pl. viii, fig. 28); *b*, *Siboganimertes weberi* (Schema).

wie grosse, kuglige Gebilde den kleinen, ventralen, birnförmigen Ganglien aufsitzen und bei weitem die grösste Masse des Gehirns bilden, kommt bei den pelagischen Nemertinen nicht vor. Die hier stattgefundenene Reduktion, die dazu führt, dass die dorsalen Ganglien höchstens nur wenig grösser sind als die ventralen, ja gar nicht selten kleiner als diese werden können, ist zweifelsohne durch das Verschwinden der Cerebralorgane verursacht, denn es sind ja diese Organe, die vor allem von den dorsalen Ganglien aus innerviert werden.' *Siboganimertes weberi* exhibits the same structure of brain as certain Pelagica, though a small cerebral organ is present.

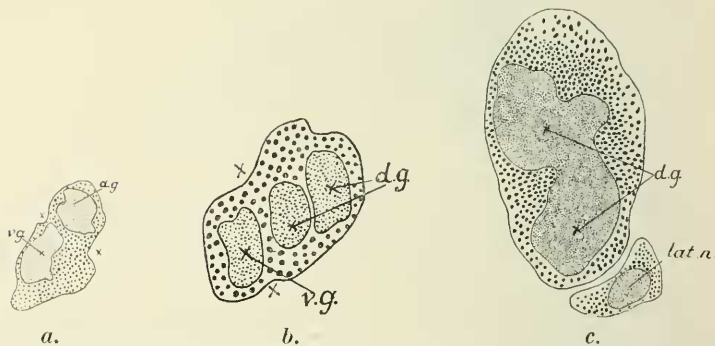
It is comparable with those in which the dorsal ganglia lie quite outside the ventral. Both have the same length, but the position of the dorsal lobe is somewhat more forward than the

TEXT-FIG. 13.



Cerebral organ of *Drepanophorus spectabilis* after Bürger (6, Pl. viii, fig. 23), Schema.

TEXT-FIG. 14.



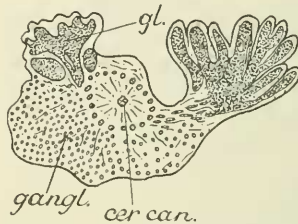
Transverse sections through the brain in the hinder region of the ventral ganglion: *a*, of *Siboganemertes weberi*; *b*, of *Drepanophorus albolineatus* of Bürger (6, Pl. xvii, fig. 3), Schema. The two crosses give the boundary of the ganglia and the corresponding places in the two genera; *c*, *Drepanophorus latus*, just after the origin of the lateral nerve-cord (6, Pl. xxiv, fig. 43).

ventral. In Text-fig. 14, *a*, the ventral lobe obtained its greatest diameter, as the nerve-cells of the nerve-cord are partly included. The two crosses give the limit of the lobes. In

Reptantia the dorsal lobe attains its greatest development in its hinder part, when the ventral lobe has disappeared. A section of *Drepanophorus albolineatus* (Text-fig. 14, *b*) to be compared with Text-fig. 14, *a*, reveals the difference between the two. The proportions have changed; instead of the ventral the dorsal ganglion exceeds in *Drepanophorus*, and if we compare a section of another form, in which the nerve-cord is seen instead of the ventral lobe, the contrast is still more obvious (Text-fig. 14, *c*). I cannot agree with Brinkmann that the disappearance of the cerebral organs caused a reduction of the dorsal brain-lobe in Pelagica. Brinkmann considers these to be descendants of true *Drepanophoridae* that have lost eyes, cerebral organs, the great development of the brain, the nephridia, the rhynchocoelomic diverticula, the anastomosing blood-vessels. As to the eyes I might agree with him: it seems quite plausible that species or even genera that live in the aphotic regions of the sea lose their eyes, as most Pelagica, *Sibogonemertes*, and *Uniporus hyalinus*, though for *Uniporus acutocaudatus* and *U. borealis* this reason cannot exist as they live in the dysphotic zone just as well. The presence of atrophied eyes in some pelagic genera, however, makes it probable that they got lost in the other. But certainly the Pelagica never possessed cerebral organs. These have developed in different ways in armed and unarmed Nemerteans. In both sub-classes we know genera without them, and these in both are primitive forms. *Callinera*, *Carinesta*, *Cephalothrix* belong to the most primitive Palaeonemerteans and they have no cerebral organs. In the Enopla this sense organ is absent in the Pelagica and in *Malacobdella*. The parasitic genus *Gononemertes* has them and in *Carcinonemertes* they seem to fail. Why must it have got lost in *Malacobdella* and *Carcinonemertes*, when it is present in the third parasitic genus? As to *Carcinonemertes*, that belongs to a non-parasitic family of *Monostilifera* with well-developed cerebral organs, it seems natural to consider the parasitic habits of the genus as the cause of their absence, though nothing is less certain. In *Bdellonemertea* this

reason is quite absent, and so it is in pelagic forms. When we can, moreover, follow the development, as is the case (1) in the Anopla, from stages like *Tubulanus pellucidus*, *Procarinina*, and other *Tubulanus* species through *Hubrechtia* to the *Heteronemerteans*, and on the other hand in *Enopla* from *Siboganemertes* (Text-fig. 12, *b*) to several *Monostilifera* (Text-fig. 12, *a*) and to *Drepanophorus* (Text-fig. 13), from (2) the irregular organ with partly free and simple constituents through the composite and irregular organ of several *Reptantia* as *Uniporus* (3, Pl. i, figs. 6 and 7) and *Drepanophorus cerinus*, *willeyanus*, *indicus* 15, 14), to the well-

TEXT-FIG. 15.



Transverse section through the cerebral organ of *Eimplectonema gracile* after Bürger (6, Pl. xxvi, fig. 41).

defined organ of *D. spectabilis* (Text-fig. 13), or from (3) *Siboganemertes* (Text-fig. 12, *b*) through stages as *Eimplectonema* (Text-fig. 15) and *Prostoma cruciatum* to *Prostoma cephalophorum* (Text-fig. 12, *a*), it seems to be rather probable that this organ has developed in *Nemerteans* and has not been inherited from now extinct ancestors. The great development of the dorsal brain-lobe is a characteristic feature of the *Reptantia*, but need not have been a possession of all *Polystilifera*. In other forms with a well-developed cerebral organ, as in *Amphiporus*, the difference of the proportions of the brain-lobes is not great, and I am rather inclined to think that the development of the sac caused the different structure of the dorsal brain-lobe of the *Reptantia*. Paired *rhyndocoelemic diverticula* are absent in all *Nemer-*

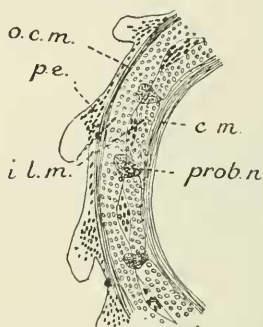
teans with the exception of Reptantia and Siboganemertes and in these they developed in different ways.¹ As in the

¹ Here seems to be the right place to mention the fact that in one species of Monostilifera the presence of paired rhynchocoelomic diverticula is noted by Bürger, i.e. *Amphiporus stannii*. However, these diverticula are quite other structures, or at least much more primitive; they are present in the nephridial region alone and are very small though wide. The musculature of the rhynchocoelomic cavity widens out at certain places. These are the sacs that have a wide lumen and open with a wide mouth into the rhynchocoelomic cavity. The muscular walls of these sacs are the regular continuations of, and just as thick as, the rhynchocoelomic wall, and a difference of structure seems not to exist. The wall of these diverticula in *Polystilifera* is as a rule much thinner, even when contracted, and we know that the mouth is provided with a sphincter, that is absent in *A. stannii*. In some unarmed genera other rhynchocoelomic diverticula, paired and unpaired, exist, but they never are comparable with those of the *Polystilifera*. *Amphiporus stannii* is a Monostilifer, as its stylet is well known. In *Drepanophorus valdiviae* (Bürger), which species has exactly the same rhynchocoelomic diverticula as *Amphiporus stannii*, the stylet is unknown; in both species these structures are restricted to the nephridial region, and in other characteristics they are very much alike too: they have no eyes, both possess small cerebral organs without a sac, behind or partly behind the brains, both have lateral nerve-cords (not ventral as in *Drepanophorus*), both have a layer of glands in the head that fails in all *Polystilifera* and is present in *Amphiporus*, both have brains that are quite different from all *Polystilifera*, with a very small dorsal and larger, perfectly separated ventral ganglia, in both the vascular system differs from that of *Polystilifera* by the presence of a dorsal loop over the brain. &c., &c. Bürger says in his monograph of the Valdivia expedition (9, p. 174): 'Leider ist aber der Rüssel nicht vorhanden, und die Organisation weist einige Züge auf, die mehr auf *Amphiporus* als auf *Drepanophorus* hindeuten; indessen ist dieses Stück dem Genus *Drepanophorus* zuzurechnen, weil sein Rhynchocölon, wenigstens im vordersten Abschnitt, laterale, einander gegenüber entspringende seitliche Aussackungen besitzt, die bisher nur von *Drepanophorus* bekannt sind.' He forgets, however, that he himself described them in 1895 in *Amphiporus stannii* in the monograph of the Nemerteans of Naples, p. 571, and Pl. xvii, figs. 5, 13, and 14. A comparison of these figures with those of the Valdivia (Pl. xxxi) gives the striking resemblance of the above-discussed species, which certainly belong to one genus, which I might mention *Valdivianemertes*. The presence of the only stylet in *Valdivianemertes stannii* (Grube) makes it certain that both *V. stannii* and *V. val-*

Pelagica no traces of a reduction in the proboscidian system are to be found, as emphatically stated by Brinkmann, we must consider this tribe as the more primitive one in the Polystilifera.

The structure of the muscular wall of the rhyncho-coelomic cavity seems to prove this. In 1914 I tried to demonstrate (18) that the proboscis and its sheath together are an invagination of the body-wall, and that all parts of the body-

TEXT-FIG. 16.



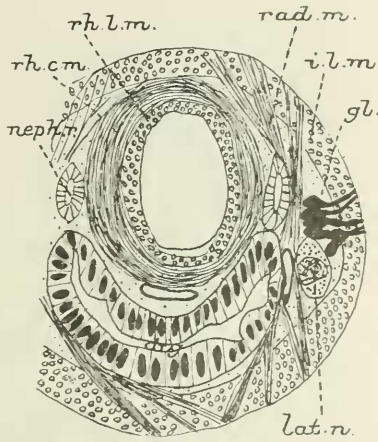
Section through the proboscis of *Amphiporus pulcher* after Bürger (6, Pl. xxiii, fig. 3).

wall are to be found in situ, either in the proboscis or in the wall of the sheath. In the Anopla this seems quite clear, but in the Enopla several difficulties arise. The presence of the third or inner muscular layer of the body-wall, which in Palaeonemerteans is characteristic, the inner circular muscle-coat (Text-fig. 1, a), has never been demonstrated, though in Drepanophorus, as I know now, its presence is quite clear in the stomodaeal region. Also the dorsoventral muscles show the same peculiarities as in the Anopla, where they are derivatives of this musculature. So it was not certain whether we had a right to look for this layer in the proboscidian system of the

diviae (Bürger) belong to the Monostilifera. Through this conclusion we have excluded *Drepanophorus valdiviae* from the Polystilifera, in which it might cause much trouble by the different structure of almost every organ.

armed Nemerteans. The other difficulty was that the spot where delamination took place seemed to be different in the Enopla. For in the unarmed Nemertini the inner longitudinal muscle-layer was split into two parts that enclose the rhyncho-coelomic cavity, which is lined by an endothelium. However, in the Hoplonemertini a circular muscle-layer lies between the longitudinal fibres and the endothelial lining of the proboscis (Text-fig. 16). I then suggested that these circular

TEXT-FIG. 17.

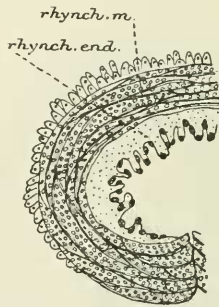


Section through *Euplectonema gracile* after Bürger (6, Pl. xv, fig. 27).

fibres are a new acquisition and do not belong to the primary proboscis, as the proboscis sheath itself is built like that of the Anopla (Text-fig. 17). *Chuniella*, one of the most primitive Polystilifera, seems to prove this supposition, as the proboscis has no circular muscles beneath the endothelium, and in Monostilifera the genus *Zygonemertes* (19) shows the same feature, as sections from South African species reveal. We knew nothing then about Polystilifera with the exception of the genus *Drepanophorus*, in which the wall of the rhyncho-coelomic cavity consists of longitudinal and circular muscle-fibres, that are interwoven (Text-fig. 18). In many Pelagica

this is the case too, as in *Siboganemertes* and all *Reptantia*; but in *Chuniella*, *Nectonemertes*, *Natonemertes*, *Para-*, *Pro-*, and *Balaenemertes* no traces of interlacing of these fibres are found, and the longitudinal layer lies next to the endothelium exactly as in the *Monostilifera* (Text-fig. 17). Brinkmann considers this kind of rhynchocoelomic musculature not as primitive, because the layers show another arrangement at the place of insertion of the proboscis. We know, however, from the *Anopla* that exactly in this part of the proboscidian

TEXT-FIG. 18.

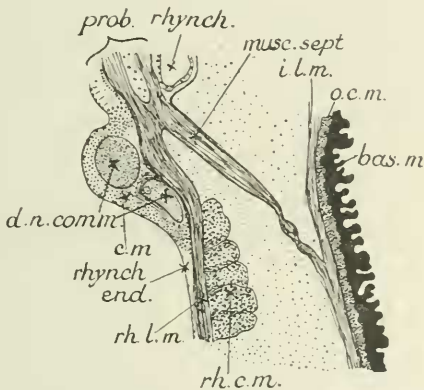


Section through the rhynchocoelomic wall of *Drepanophorus* after Bürger (6, Pl. xxiii, fig. 37).

system the first traces of the new outer longitudinal layer appear, when the middle part holds the older structure; that here other layers disappear first, that in other species fail absolutely and in more primitive genera are present in all parts; that at this spot new constrictors and retractors can develop, that in most species are unknown, to be short, that all changes start in this part of the proboscidian system. When we remember, moreover, that this spot is the place where originally the invagination of the whole system took place, that by the development of the precerebral region, as will be discussed later, the continuity with the body musculature was broken, 'Muskelseptum, Rüsselfixatoren' originated, 'Seitenstamm-muskeln' developed: that the inner circular muscle-layer is and must be present in the rhynchocoelomic wall, but almost disappeared in the body-wall; that originally here the central

nervous system was found embedded in the longitudinal musculature, as seems still to be the case in some species (Brinkmann, 4), and that its place changed in the different genera, then we understand that we cannot look for primary conditions in this part of the proboscidian system. That the longitudinal musculature of proboscis and sheath are in contact with each other at the place of insertion is quite natural (Text-fig. 19), while they both are part of originally one layer and from one place take their origin.

TEXT-FIG. 19.



Dorsal part of a longitudinal section through the anterior region of *Balaenanemertes musculoaudatus* (Brinkmann) with protruded proboscis (4, Pl. 15, fig. 10).

Brinkmann's statement that the brains of *Pendoneurtes* and *Balaenanemertes* are situated in the middle of the musculature of the proboscidian system is of the greatest importance; for we know from *Drepanophorus* that the longitudinal musculature is in contact with the same parts of the body-wall by a muscular septum, which separates the precerebral or head-region from the brain and the body and always expands just before the ganglia. In the *Pelagica* this septum as a rule is broken up into several muscles which Brinkmann calls 'Rüsselfixatoren' and that as a rule lie outside and before the nerve-ring. The brain lies at the same

place as the nerves of all Enopla, on the inner side of the inner longitudinal musculature. So we have to look for the inner circular muscles of these genera behind the brain, and not before it. If we ask where the brain lies exactly in *Pendoneimertes* and *Balaenanemertes*, Pl. v, fig. 1, Pl. xiv, fig. 19, Pl. xv, figs. 3 and 4, Pl. xvi, figs. 17 and 18, of the monograph (4) show us that it really is found between two layers of longitudinal musculature. Whether the outer layer consists of strands that go to the body-wall ('Rüsselfixatoren') or of the inner parts of them that still have to join the wall of the cavity, is not clear. But in any case it is certain that we can expect the inner circular muscle-layer only behind the brain and not before it. Wherever Brinkmann describes the exact relations of the muscle-layers in these parts, it invariably is mentioned that the first traces of the outer circular musculature of the proboscis sheath are found behind the brain. This cannot always be so, for I know cases in the Reptantia where the remains of the circular musculature of the body-wall are found around the hinder parts of the brain, and in this case it is evident that the contact with the rhynchocoelomic part of this layer must be looked for before the brain. In such cases we must expect the outer circular musculature of the sheath to be in the nerve-ring. In others I noted the same beginning of this layer as Brinkmann, i. e. behind the nerve-ring.

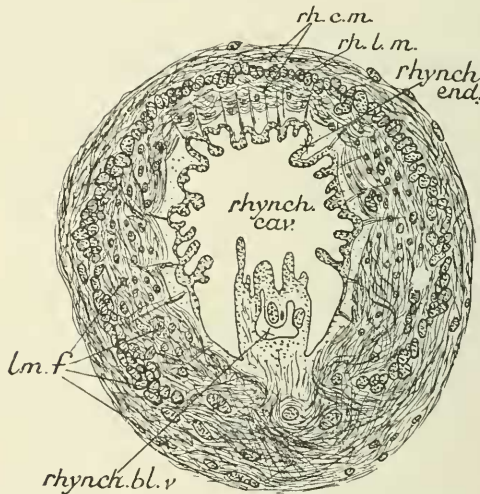
The wall of the cavity before the brain is built differently in different cases. It is interesting to note that in one Malayan species all circular muscle-fibres are absent in front of the brain, in another all longitudinal, and always the interlacing begins behind the nerve-ring. Brinkmann describes in all his genera of *Pelagica* the presence of an inner circular muscle-layer (as the direct continuation of the new proboscidian layer) before the brain and outside of it a longitudinal layer which, he says, passes through the circular musculature behind the brain and so comes to lie inside (Text-fig. 19). If, however, this really was a passing through we should find an interlacing of fibres at this place. Though Brinkmann is very exact in his statements he never mentions this, and his figures show

everywhere a very distinct border of the musculature (Text-fig. 19). Pro- and Parabalaenanemertes, Balaenanemertes, Nato-, Neetonemertes, and Chuniella show us this type of rhynchocoelom, as found in all Monostilifera too, and so does the greater part of the sheath of Pelagonemertes. The development of a third layer, which might be indicated where the proboscis is affixed, never took place, as I will now demonstrate.

The interlacing of circular and longitudinal muscle-fibres, which in Pelagonemertes took place in the hinder part of the rhynchocoelomic wall, is found in the genera *Protopelagonemertes*, *Plotonemertes*, *Pendonemertes*, *Mergonemertes*, *Paradino-*, *Phallo-*, *Crasso-*, and *Planktonemertes*. in all Reptantia and in *Siboganemertes weberi*. Whether the new circular muscle-coat of Brinkmann is present or not we cannot decide in these genera; in Pelagonemertes it certainly is absent, and in the Malayan species referred to above the interlacing took place between the two original layers, as I will describe in *Siboganemertes*. The proboscis has a thin outer circular muscle-coat and a thick longitudinal coat, but the new layer is absent. The precerebral septum which connects the longitudinal musculature of the body with the rhynchocoelomic wall and proboscis lies exactly in front of the brain. Inner circular muscle-fibres between this septum and the endothelial lining of the cavity of the sheath fail absolutely; a great quantity of fine mesenchymatic fibres, which stain quite differently and are found at many places in the body parenchyma too, lies inside the endothelium and between these the first longitudinal fibres are embedded. Outside of these the first circular fibres appear behind the nerve-ring and they are very few. The whole muscular wall is thin and, in the ventral part, disappears but for a few longitudinal fibres. It is, however, quite clear that in the proximal part an interlacing of fibres takes place, and here certainly the new circular layer has not developed. It is absent in the proboscis too. From the results obtained in *Siboganemertes*, and from similar facts in some Drepanophoridae and in Pelagonemertes, I might conclude that the development of

the wall of the sheath in Pelagica took place in the same way. Primary are the stages with two muscle-layers, as Chuniella, &c. The first stages of interlacing are given in Armaueria and Dinonemertes (Text-fig. 20). In these genera started the penetration of the circular muscle-coat by the longitudinal fibres, or vice versa; but the longitudinal musculature has not yet reached the outside. We see an interlaced inner wall, a longitudinal middle coat, and outside of it a circular layer.

TEXT-FIG. 20.



Transverse section through the rhynchocoelomic cavity of *Dinonemertes alberti* (Brinkmann) (4, Pl. vii, fig. 13).

As *Dinonemertes* seems to be connected with *Mergo-*, *Phallo-*, and *Paradinonemertes* and *Armaueria* with *Pendonemertes*, I might rather solve the problem of these genera as the beginning of the interlacing, which is completed in *Protopelago-*, *Ploto-*, *Pendo-*, *Crasso-*, *Plankto-*, *Mergo-*, *Phallo-*, and *Paradinonemertes*.

Pelagonemertes kept the more primitive stage in the proximal part of the sheath, which fact seems to point to the hinder part of the cavity as the place of origin of the interlacing. *Bürgeriella* gives still a higher development that confirms these

views, as it is the most specialized genus of the Pelagica in many respects. The distal part acquired an inner circular layer, as the originally outer circular coat after the stage of interlacing, shown still in the proximal part, lost its longitudinal fibres which all lie outside of it. This is in accordance with the other anatomical facts, that make us look for the nearest relations of this aberrant genus among species with a basket-like structure of the sheath; proximally it is basket-like in *Bürgeriella* too: the distal part has an inner circular and an outer longitudinal layer. Compared with Text-fig. 20 of *Dinonemertes* the position of the fibres is this, that the whole circular muscle-coat traversed the longitudinal one (in *Dinonemertes* only the inner parts) and so came to lie inside. Other traces of an inner circular muscle-coat fail, and as *Bürgeriella* evidently is a highly specialized genus it would be rather incomprehensible why it should be the only one that had beheld this primitive feature on Brinkmann's explanation of facts.

The other support of Brinkmann's theory of a third muscle-layer of the wall of the sheath is *Protopelagonemertes*, in which genus the interlacing of fibres is already found in the nerve-ring. However, if we suppose, as I do, that the interlacing starts in the hinder part of the cavity and goes on from behind forwards, as shown in *Bürgeriella* and *Pelagonemertes*, every reason fails why the interlacing should stop with the brain as the nerve-ring lies in the muscular septum. *Protopelagonemertes* bears its name quite undeserved, as *Pelagonemertes* seems not to be related to it and is also to a certain extent more primitive.

The result of this discussion is that the genus *Chuniella*, which after Brinkmann's description must be one of the most primitive genera if not the most primitive genus of the *Polystilifera*, perhaps even of the *Hoplonemertini*, has a proboscis with exactly the same muscular layers as all primitive *Anopla*, *Malacobdella*, and some *Monostilifera*, and as *Siboganeemertes weberi*, the most primitive genus of the *Reptantia*; that also the wall of the sheath in this genus is

built like that of all Anopla and of all Monostilifera, and that this wall in the Polystilifera is found in the pelagic genera *Nato* and *Nectonemertes* and the family *Balaenanemertidae* as well. That the interlacing of these two original muscle-coats, which is characteristic of all Polystilifera Reptantia and elsewhere is unknown, is also found in many Pelagica; that the process of interlacing seems to start in the hinder part of the rhynchocoelomic cavity and proceeds proximally, as shown in *Pelagonemertes*. That we see the penetration of the two layers go on in *Dinonemertes* and *Armaueria*, and that the interlacing is completed in all other genera of Pelagica and in the Reptantia. That in one genus this process resulted in the inversion of the original layers, i.e. the aberrant genus *Bürgeriella*, where the proximal part of the sheath has the basket-like structure characteristic of Polystilifera, and the distal part, as in *Pelagonemertes*, shows the result of this process.

If we look at the digestive tract three remarkable points are to be distinguished. The position of the mouth under the brain was stated to be very primitive in armed Nemer-teans and even in Polystilifera to be quite unusual. As to the oesophagus we have the statement of Brinkmann that this part of the stomodaeum is absent in all Pelagica with the only exception perhaps of *Planktonemertes*. His fig. 23, Pl. xiii (4), gives no right to compare this small oesophagus with that of *Siboganemertes* (Text-fig. 11): after his description on p. 24, however, we can hardly speak of an oesophagus, and truly can say in Pelagica the oesophagus is absent, as in the unarmed genera. But in the Reptantia a well-developed oesophagus is always, in the Monostilifera, as a rule present. We know its absence in *Amphiporus marmoratus* (Bürger) (6, Pl. xvi, fig. 1), though in *Amphiporus marmoratus* (Joubin) it is well developed as in most other species (12, p. 564, fig. 4). This figure interests us still more because the different parts of the stomodaeum with the exception of the oesophagus show about the same features as *Siboganemertes*. The pyloric tube of Joubin's species is much wider than in our specimen, but it opens into the gastric cavity at the same

place. What is the continuation of the oesophagus in *A. marmoratus* (Joubin) is the ventral unpaired diverticulum of *Siboganemertes*, and the true gastric cavity lies enclosed between the pyloric tube and the ventral diverticulum. All parts of the stomodaeum are unpaired in *Siboganemertes* but the intestinal blind-gut shows at the side of ventral unpaired pouches paired lateral diverticula that are longer than the blind-gut itself, as in *A. marmoratus* (Joubin). Nothing of this kind was ever found in *Polystilifera*, though some very interesting features are known from Brinkmann's studies on the bathypelagic species. Not only do they show the absence of an oesophagus, but the whole stomodaeum is very short and much less differentiated. In almost all his figures the pylorus is already shown beneath the brain, and as a rule the blind-gut extends till here. In fig. 9, Pl. xv, a longitudinal section shows the short and narrow gastric cavity of *Balaenemertes musculocaudatus*: fig. 13, Pl. xii (Text-fig. 26), gives the same features in *Nectonemertes primitiva*, and Brinkmann states that in *N. minima* the epithelium of the gastric cavity is unfolded, the cavity still narrower and shorter. Brinkmann takes these forms as the most reduced ones. However, how can we explain these differences in the same structure within a monophyletic group, as the *Polystilifera* certainly are, the highly differentiated gastric cavity of *Siboganemertes*, the quite differently but not less highly developed structures of the *Drepanophoridae* and the more or less simple stomodaeum of the *Pelagica*, if we do not suppose these to be primitive?

The stomodaeum in armed Nemerteans is a structure different from that in the Anopla, as is shown by its development and by the presence of an entodermal blind-gut in the first. We know it to be a simple structure, a mere narrow tube in *Otopyphonemertes*, in *Zygonemertes* it is not much more; we know that the oesophagus is absent in *Geonemertes*, in *Stichostenma*. Why then must the *Pelagica*, that have the same peculiarities, have developed from highly differentiated forms as *Drepanophorus*? On the contrary we see here how the simple

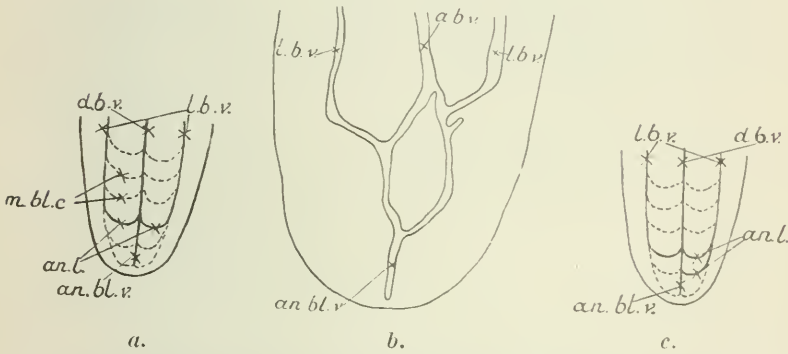
invaginating stomodaeum with a few glandular cells only develops into a gastric tube that opens only a short distance behind the beginning of the enteron, as in *Balaenanelmertes musculoecaudatus* or *Nectonemertes*. With the greater development of the stomodaeum the different parts become better differentiated, in the first place gastric cavity and pylorus, and this can be obtained in different ways, as shown by *Siboganemertes* (Text-fig. 11) and *Drepanophorus* (Text-fig. 8), or by *A. marmoratus* (Joubin) and *A. marmoratus* (Bürger); the Pelagica provide us with a whole series of stages in this development. Thirdly an oesophagus is differentiated, which all Pelagica lack and often even other groups. So *Siboganemertes* with its diverging structure of the digestive system is not as primitive as the pelagic forms; but it cannot be included in the *Drepanophoridae* either, as the development goes in a different direction.

The vascular system shows a very primitive type, as in *Siboganemertes* there are no anastomosing vessels with the exception of the cephalic loops. The cephalic vessels bend into the nervous ring of the brain in the ordinary way and a dorsal vessel is present, as far as sections were made; but it is not in contact with the rynchocoelomic cavity. The absence of metamericly situated vascular loops is known in *Uniporus*, in *Reptantia*, and in all Pelagica. The occasional presence of a double anal loop in an abnormal individual of *Pendonemertes levinsemi* (Text-fig. 21, *b*) and the existence of a blind dorsal median vessel in the tail arising from the anal loop, makes it at first sight rather plausible that the reduction series as given by Brinkmann on p. 163 of his monograph (4) gives a true account of the facts. But when we know that in primitive Anopla the anastomosing vessels are absent, that they fail in *Uniporus* (in which genus even the anal loop should be absent) (3), and that they fail in *Siboganemertes*, we become sceptical to the explanation of their absence in Pelagica. Moreover the reconstruction of the tail of *Pendonemertes* on p. 20 (Text-fig. 21, *b*) and the scheme on p. 163 (Text-fig. 21, *c*) are rather different, and it seems not at all certain that the hinder vessel

is the continuation of the lateral vessel; the course of the blood-vessels seems too irregular to decide anything from this single abnormality.

Another interesting fact in *Siboganemertes* is the absence of any connexion between the dorsal vessel and the rhynchocoelomic cavity. This is known from one form of *Polystilifera*, *Armaueria fusca*. The *Monostilifera* exhibit the same feature in some *Prostoma* species (*P. amphiporoides*, *duboisii*, *antarcticum*, *gulliveri* (Bürger)), and it is found in *Malacobdella*. Wherever a dorsal blood-vessel exists

TEXT-FIG. 21.



Blood-vascular system in the tail of *Pendonemertes levinsoni*. *a*, Schema of normal individual after Brinkmann (4, p. 163, Text-fig. 29, II); *b*, abnormal individual (4, p. 20, Text-fig. 4); *c*, schema of this abnormality (4, p. 163, Text-fig. 29, III).

in the unarmed forms, it is in connexion with the rhynchocoelomic cavity (Text-fig. 20), though other special rhynchocoelomic vessels may be present. In most Palaeonemertean, however, the dorsal vessel is quite absent. This is a rare case in *Hoploneimertini*, and, as far as I know, it has been described in *Pelagonemertes moseleyi*, *Balaenemertes chuni*, and *Carcinonemertes carcinophila*. Brinkmann, guided by the opinion that the *Pelagica* are reduced *Drepanophoridae*, considers these forms

as the most advanced ones: I, however, believe that the formation of a dorsal blood-vessel takes place in the Pelagica; that it has been formed in two ways, either in relation to the rhynchocoelomic cavity, or quite separately. This last way is represented in three aberrant genera. *Armaueria* in the Pelagica, *Malacobdella*, the *Bdellonemertean*, and *Siboganemertes*, the representative of a new group of Reptantia. Perhaps other genera passed this stage to acquire a rhynchocoelomic vessel afterwards, as might be plausible in *Prostoma*. Some genera, however, seem to have got this rhynchocoelomic vessel directly, as is shown in *Pelagonemertes rollestoni* and the nearly related genus *Natonemertes* with a short, blind-ending proboscidian blood-vessel, or in the family of the *Balaenanemertidae*, where a dorsal vessel is absent in *B. chuni*, and in other species of the same genus a blind rhynchocoelomic vessel is present as well as in *Probalaenanemertes* and *Parabalaenanemertes*. Another fact of interest in the blood-vascular system, and which seems to demonstrate how the organisms of this group try to obtain a certain result in different ways, is the development of what Brinkmann calls 'Ovarialschlingen'. He demonstrates in *Dinonemertes investigatoris* that the lateral blood-vessels in the gonadial region make large, irregular loops between the ovaries and the entodermal sacs. These loops that convey the nutrition from the sacs to the ovaries are absent in all other forms; but I found them also in *Siboganemertes*. It is supposed that the vascular loops between the dorsal and lateral vessels of other Nemerteans have the same purpose, and Brinkmann remarks that this fact states Dollo's law of irreversibility, as the regular loops that once disappeared did not return, but another structure took on the same function. What we find in *Dinonemertes* and *Siboganemertes* can perhaps just as well be the beginning of what results in vascular loops between the vessels. So everywhere I reach the same result; the Pelagica show the development of every organ, from the primitive stages known in Palaeonemerteans to the specialized features of Drepanophoridae and Monostilifera; the

development supposed by Brinkmann seems to have taken place in the reverse direction: what he calls highly reduced, I call primitive, and vice versa.

This disagreement does not extend to the nephridial system: for this is present in all Nemerteans without exception that do not belong to the Pelagica. That it has not yet been found in *Prosadenoporus* must partly be due to the highly developed head-glands that extend into the nephridial region, partly to the smallness of the canals or the preservation. As all Platyhelminths possess a well-developed nephridial system, we are obliged to explain its absence in the Pelagica by reduction. In *Sibogonemertes* nephridia are present, but of a type that differs from that of the Reptantia. A large efferent duct is present at each side, extends behind the real nephridium, and has a more caudal, lateral mouth. The nephridia lie at the side of the dorsal brain-lobes and the cerebral organs, and just behind these obtain their greatest development. The ducts open laterally behind the end of the pyloric tube. This type is known from primitive Anopla, a well-localized system of canals with a long efferent duct, quite different from the other types of nephridia that extend through the whole body in the same way and have one or more short ducts. In the Reptantia also it is much less circumscribed, extends as a rule from the end of the brain along the stomodaeal tract, and has one efferent duct that can take its origin in any part of the system and opens directly to the exterior. Our knowledge of *Monostilifera* is as yet too incomplete to understand the value of these facts.

The gonads, however, seem to be much more interesting. The only individual of *Sibogonemertes* happened to be a male with well-developed testes, a fact of the greatest importance, as the Pelagica exhibit an extraordinary feature in the position of these glands that is characteristic of the group.

As a rule the gonads lie, be they ♀ or ♂, in the intestinal region in armed and unarmed Nemerteans. The only exception are the testes of the Pelagica that never are developed in this region, and always lie before it, directly behind, at the side of,

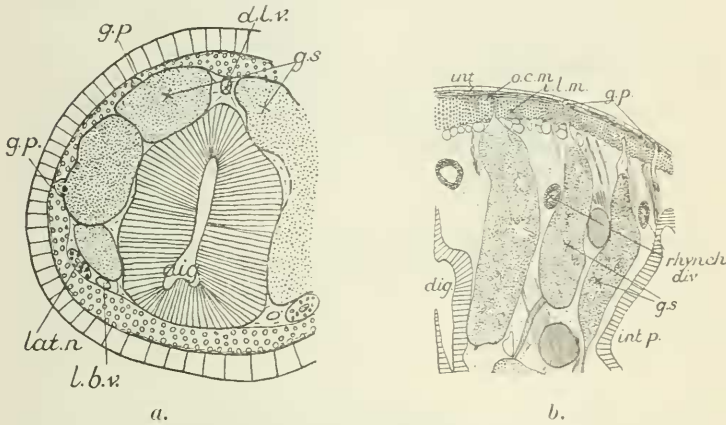
or even before the brain. The ovaries are developed in the usual way. These facts can easily be understood as we know the testes of Platyhelminths to be developed all over the body. The arrangement of the gonads in primitive Anopla without intestinal pouches is absolutely irregular, as shown by Bürger in *Tubulanus* (8, Pl. iv, fig. 2). Two interesting facts are to be mentioned: the gonads are placed in several irregular rows, and the gonopores lie on the dorsal surface. In the Anopla we can follow the development from this stage without intestinal diverticula to the pseudo-metameric arrangement in *Lineus* and *Cerebratulus*, where always one gonadial sac lies between two intestinal pouches, opening to the exterior by one row of dorsal gonopores.

In Enopla the Bdellomorpha display the same irregular position, as for instance *Tubulanus polymorphus*, and have dorsal gonopores. The Hoplonemertini show a great variety of arrangement. First we have to look at the Monostilifera, of which *Geonemertes*, *Nemertopsis* (Text-fig. 22, a), *Prosadenoporus*, *Prosorochmus* have a number of gonads between two following intestinal pouches, the first stage of arrangement that follows on the above-described displacement of *Tubulanus polymorphus* in the Anopla. All these worms are more rounded than the flat *Malacobdella* and the *Tubulanidae*. In consequence the gonopores partly lie more laterally, but always above the nerve-cords. The next stage is the reduction of the number of gonads per pseudomere to one on each side, as in *Prostoma coronatum* (8, Pl. ii, fig. 3) and *Amphiporus* species. At last we get a still greater reduction of this number as in *A. pulcher* (8, Pl. xiii, fig. 6).

In the Polystilifera we know two genera of Reptantia. *Uniporus* and *Drepanophorus*. *Uniporus* (Text-fig. 22, b) has in each pseudomere two to five gonadial sacs with dorsal pores and exhibits in consequence a very primitive feature. In *Drepanophorus* we know the great regularity in which intestinal pouches and gonads alternate, one sac between two pouches. But the gonopores lie laterally (Text-fig. 23, a) as in *D. willeyanus*, *cerinus*, *indicus*, or ventrally

(Text-fig. 24, *D. albolineatus*). Moreover, these sacs have, as Punnett (14, 15) showed, a peculiar form. In more rounded species, as the first, they are V-shaped (Text-fig. 23, *a*) with the two legs above and beneath the intestine and the lateral gonoduct at the place of junction of the legs. In *Siboganemertes* this is found too, but the sperm is not developed in this large sac alone. Peripherally small sacs are found

TEXT-FIG. 22.



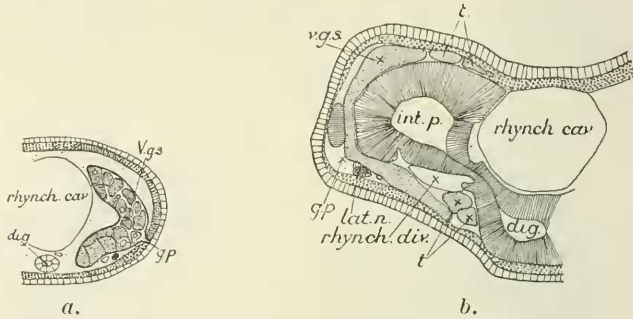
Sections through gonadal region: *a*, of *Nemertopsis peronea* after Bürger (6, Pl. xv, fig. 5); *b*, of *Uniporus hyalinus* after Brinkmann (3, Pl. 1, fig. 5).

(Text-fig. 9) which open into the central V-shaped sac (Text-fig. 23, *b*). Bürger found the same development of ovaries in *Drepanophorus albolineatus* (Text-fig. 24), one egg in each sac; but in other species the central sac itself is filled with eggs or sperm (Text-fig. 23, *a*). It seems to me that the small sacs are comparable with the gonadal sacs of *Uniporus*, *Geonemertes*, *Tubulanus*, *Malacobdella*, and that the central V-shaped pouch is a new growth in the *Reptantia* and *Siboganemertes*. The epithelium of the central pouch, whether it is simply a new gonoduct or the invaginated ectoderm with the original gonopores, acquires later the function of the gonadal epithelium and the original gonads disappear. In

each case we see the tendency of the gonads, whether testes or ovaries, to arrange themselves metamerically and become reduced in number.

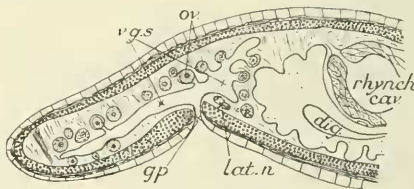
In the Pelagica the differences of sexes are greater. The

TEXT-FIG. 23.



Sections through the gonadial region: *a*, of *Drepanophorus willeyanus* (Punnett) (14, Pl. lix, fig. 20); *b*, of *Siboga-nemertes weberi*.

TEXT-FIG. 24.



Section through *Drepanophorus albolineatus* with an ovary after Bürger (6, Pl. xxvii, fig. 52).

ovaries are metamericly developed, never more than one between two intestinal pouches, but the gonopores lie on the ventral side. This may be the case in *Drepanophorus* too (Text-fig. 24). In broader and flattened forms the body becomes thin with flat edges, outgrowths of the body-wall and parenchyma, that in certain species contain no organs at all, in others rhynchocoelomic diverticula only. In some of these species it is quite obvious that the outgrowth took place above the

lateral gonopores, that in this way became ventral (Drepanophoridae-Siboga expedition); the V-shaped gonadial sac still is quite clear. In *D. albolineatus* (Text-fig. 24) the gonad acquired another, third part, that lies in this 'Seitenrippe'; and the ventral primary leg was somewhat reduced; but all three parts are present. In the Pelagica the development of the ventral ovaries cannot have taken place in this way, as all traces of the V-shaped sac or of many ovaries are absent, and real dorsal gonopores are unknown in both sexes. The only cases, as far as our present knowledge goes, in which the gonopores are not ventral but lateral seem to be the testes of *Armaueria* and *Parabalaenanemertes*, and even in these the testes open partly ventrolaterally. As to the ovaries they are rather uniformly built, and there is a reduction of the number of eggs, which grow very large and contain much yolk. The ovaries are so small that it seems unnatural to derive them from the large sacs of true Reptantia; it is more justifiable to compare these gonads with the smaller sacs of *Uniporus* and other *Hoploneimertini* that are reduced to one pair per pseudomere, or even to less as in *Pelagonemertes* and other genera. That the ovaries secondarily migrate into a more central position is shown by Brinkmann in one case; the young ovaries lie outside the peripheral lateral nerves and when they become older grow inside and become a tube. This tube may bend over the nerves to the inside of them; but always the origin of the sacs seems to be at the outside of the nerves. The medioventral gonopores of *Balaenanemertes*, *Probalaenanemertes*, *Pelagonemertes*, and *Armaueria* may take their origin from the inner leg of such forms, though it may just as well be possible that in Pelagica the more central position of the nerve-cords as compared with those of other *Hoploneimertini* for the first time make the displacement of the gonopores to the middle line possible.

The development of the testes proceeds in two distinct ways. Instead of being present in the middle and hinder parts of the body like the ovaries, they are found only in the anterior part from the brain to the enteron, and in some cases even

before the brain. Brinkmann showed in his monograph that this characteristic seems to be a most important fact in the propagation of the species, coinciding with the development of copulatory organs. In this part of the body the pseudomeric arrangement is not so well developed or is even absent as it is in the stomodaeal part, and only the entodermic blind-gut can show metamERICALLY arranged diverticula. In the genera in which testes are known these are arranged in two ways : (1) with a tendency to metameric arrangement (only behind the brain) in *Plotonemertes*, *Paradinemertes*, *Phallonemertes*, *Chuniella* and *Dinonemertes*, *Bürgeriella*. *Chuniella*, with its long irregular rows of testes, seems to be the most primitive ; the influence of the diverticula of the blind-gut is seen here as well as in *Bürgeriella*, where they lie more irregularly but are less in number. *Plotonemertes* represents the next stage, and the regularity seems to be perfect in *Phallonemertes*, *Paradinemertes*, and perhaps in *Dinonemertes alberti*. (2) In the other group the irregularly placed testes show a tendency to discharge the sperm as near to the head as possible and to form clusters. The effect of this arrangement is shown by Brinkmann. In *Nectonemertes* with its tentacles the testes lie in two irregular rows behind and at the side of the brain, but long gonoducts have developed (Text-fig. 25) that all point to the head ; they are still more forward and irregular in *Armaueria* ; in *Natonemertes* a pair of irregular clusters lies just beneath the brain, and in *Para-* and *Balaenanemertes* the clusters lie at the side of and before the brain and have their gonopores all directed to the proximal edge of the body. *Pelagonemertes* shows the same features as *Balaenanemertes*. So the gonads of the *Pelagica* developed quite differently from those of all other Nemerteans.

The result of the examination of the anatomical features of the *Pelagica*, the *Reptantia*, and *Siboganemertes* in these pages is :

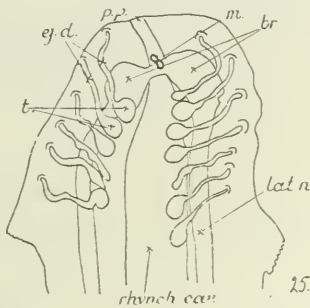
1. That the division of the *Enopla* into *Polystilifera* and *Monostilifera* is well founded, as not only the differences in the armature of the proboscis exist, but also the way in which the

connexion between proboscis pore and mouth can be formed differs in these sub-orders.

2. That the Polystilifera exhibit the more primitive features, as in most genera the proboscidian and digestive systems are quite separate from each other, and the mouth even can be found underneath the brain as in Siboga- and Paradino-nemertes.

3. That in the Polystilifera the Pelagica are the more primitive, though a specialized tribe.

TEXT-FIG. 25.



Position of testes and ejaculatory ducts on the ventral side of *Nectonemertes minima* (Brinkmann) (4, p. 104. Text-fig. 23).

4. That the absence of cerebral organs, of a highly differentiated brain, of a long much-developed stomodaenum with oesophagus, of rhynchocoelomic diverticula, of metamERICALLY arranged vascular loops, are primitive features, and that reduction did not cause them.

5. That the development of the musculature of the proboscis and its sheath in all Hoplonemertean is in perfect accordance with our knowledge of the anatomy of the Anopla and of their embryology, and that every stage of this development from the Anopla stage to the interlacing of Drepanophorus is found in the different genera of Pelagica.

6. That the blood-vascular system in the different genera of Pelagica shows the development of the dorsal blood-vessel from a short blind rhynchocoelomic vessel, that in some species

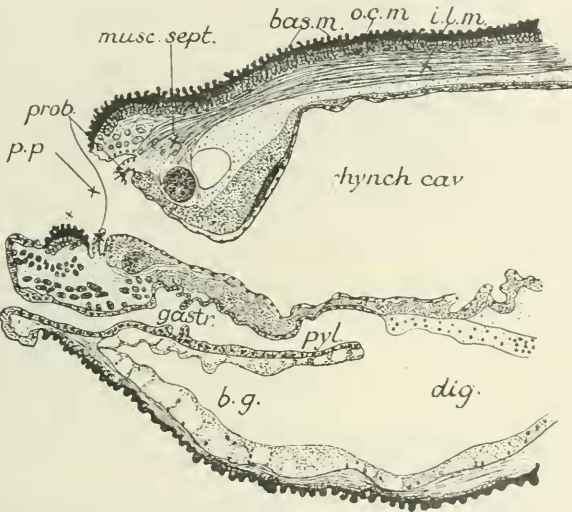
still is absent, to a large vessel, that communicates in the tail with the lateral vessels.

7. That the reproductive system shows quite a number of characteristic features that are unknown in all other Nemerteans and cannot have developed from stages known in Monostilifera and Anopla, nor from those in the Reptantia; that the influence of the pelagic habits, which caused reduction of the number of eggs as these grew larger, and copulation, cannot account for all these facts, though the ventral position of the gonopores may be due to it.

Here I might call attention to another fact of importance. If we look at the figures of the pelagic Nemerteans it must be evident to everybody, especially on comparison with illustrations that give the anatomy of the whole animals, that the region we call the head in other Nemerteans, or the precerebral region, is absolutely absent. As already stated above, the insertion of the proboscis and the muscular septum before the brain mark the place where originally the invagination of the proboscidian system took place. This we see actually in the pelagic forms; the rhynchodaeum is only very short and there is no true head region (Text-fig. 26). Brinkmann states several times that the rhynchodaeum may be extremely short, and only in this way can we understand a dorsal migration of the proboscis pore that comes to lie above the brain as in *Armaueria* or *Parabalaenanemertes*. In the primitive genus *Siboganemertes* the precerebral region is extremely short too, and the broad line which demarcates the proximal end of the animal reminds one of the same feature in the headless Pelagica. The brain lies directly behind the septum, i. e. quite terminally, as seen in all the illustrations of Brinkmann. A comparison of Text-figs. 25 and 26 with Text-figs. 2, 3, 6, and 8, shows this very clearly. In the armed Nemerteans a displacement of the mouth goes hand in hand with the development of the head, and in consequence of this the development of the stomodaeum and oesophagus. If we understand the head region of Nemerteans in this way the difference in the structure of the body-wall before and behind the brain at once becomes

clear, and the presence of muscle-strands in the snout can be understood also. The newly developed region could only get some small outer layer of the musculature as the bulk of the muscular coat is used by the formation of the proboscidian system. So we find the greater part of the longitudinal musculature as the septum before the brain or as proboscidian muscles,

TEXT-FIG. 26.



Longitudinal section through the anterior region of *Nectonemertes primitiva* (Brinkmann) (4, Pl. 12, fig. 13) to show the total absence of a head and rhynehodaeum. The proboscis is lost and the stomodaeum protrudes through the mouth. The tip of the snout is indicated by a cross.

and only a very thin layer of longitudinal fibres is seen to accompany the epithelium and the few circular fibres underneath. That in this process of division of the musculature some longitudinal fibres are found in the parenchyma of the snout that connect the musculature of body-wall, rhynehodaeum, and septum seems to be quite natural. The aberrant structure of the head of all Nemerteans as far as concerns the musculature can only be understood in this way.

Even in this feature the Pelagica are very primitive in the absence of a true snout.

With regard to Siboganemertes we have to state the following facts :

The presence of cerebral organs, rhynchocoelomic diverticula, an oesophagus, nephridia, metamERICALLY arranged male gonads brings it in near relation to the Reptantia.

However :

1. The position of the mouth under the brain is more primitive than in any of these genera.
2. The absence of a snout, present in other Reptantia, recalls this characteristic of the Pelagica.
3. The proboscis has but two muscular layers, and not three as in Reptantia and Monostilifera.
4. The rhynchocoelomic diverticula lie on the inside of the entodermal diverticula and never peripherally as in the other Reptantia.
5. The brain is most primitive, as in Pelagica, without large, free, dorsal lobes.
6. The cerebral organs are the most primitive we know in Hoplonemertini, consisting of free independent parts, without a bifurcation of the canal characteristic of the Drepanophoridae.
7. The digestive tract has a short bulb-like oesophagus.
8. The stomodaeal parts are much more highly developed than in the other Reptantia, displaying the same features as in certain Amphiporus species, and all parts are distinctly and sharply separated from each other, as is never the case in other known Polystilifera.
9. The entodermal blind-gut has unpaired diverticula.
10. The nephridia are different from those of the Reptantia.
11. The lack of metameric blood-vessels is a primitive feature in common with all Pelagica and Uniporus.
12. The dorsal blood-vessel never lies in the rhynchocoelomic cavity, a rare feature known in Armaueria in the Pelagica, in Malacobdella and in some Prostomas in the Monostilifera, but unknown in Reptantia.

13. The testes consist of many small peripheral sacs that open into a large V-shaped sac as known in the Drepanophoridae only, and representing probably a more primitive stage than that of most Drepanophorus species.

Every organ of *Siboganemertes* is either more primitive than in the other Reptantia or quite differently developed (rhyncho-coelomic diverticula, digestive system, nephridia, dorsal blood-vessel). We must include it in the well-defined group of Reptantia as given by Brinkmann. On the other hand we cannot include this genus in his family Drepanophoridae, nor in the Uniporidae or any other family of the Siboga material. The real relationship between the known Drepanophoridae and *Siboganemertes* we can only indicate by dividing the tribus Reptantia (Brinkmann) into two subtribus, the Archireptantia and the Eureptantia, of which the first contains the family Siboganemertidae and the other the different groups of Drepanophoridae as yet known.

The diagnoses of the different systematic divisions of Enopla are as follows :

Sub-classis Enopla (Max Schultze).

The body-wall consists of a one-layered epithelium, a basement membrane, a circular muscle-layer, and an inner longitudinal muscle-coat. The nervous system is embedded in the body parenchyma. Cerebral organs, where present, separated from the brain. Proboscidian and digestive system show a tendency to acquire a common mouth. Blood-vascular system without lacunae.

Ordo I. Bdellomorpha (Verrill).

Parasitic Nemerteans with a sucker. The proboscis is inserted in the wall of the digestive system ; without armature. Digestive tract a more or less winding tube without diverticula and blind-gut. Blood-vessels highly branched.

Ordo II. Hoplonemertini (Hubrecht).

Proboscis armed. Digestive system with blind-gut and paired diverticula ; straight. Vascular system without tree-

like branching : as a rule with metamerically arranged loops between the three longitudinal vessels.

Sub-ordo I. *Polystilifera* (Brinkmann).

Hoplomertini with many stylets on a crescent-shaped base. Proboscis pore and mouth are separate or open separately in a common atrium. The muscle-coats of the rhynchocoelomic cavity interlace and become complicated as a rule.

Sub-ordo II. *Monostilifera* (Brinkmann).

Hoplomertini with one stylet on a handle-shaped base. The mouth opens into the rhynchodaeum. The rhynchocoelomic wall never shows interlacing, and consists of an inner longitudinal and an outer circular muscle-coat.

The sub-ordo *Polystilifera* contains the following groups :

Tribus I. *Pelagica* (Brinkmann).

Pelagic *Polystilifera* without a distinct snout. Cerebral organs, nephridia, rhynchocoelomic diverticula, metameric blood-vessels, and oesophagus absent. Testes only in stomodaeal region. Gonopores ventral.

Tribus II. *Reptantia* (Brinkmann).

Polystilifera with cerebral organs, rhynchocoelomic diverticula, nephridia, and oesophagus, and with metamericly situated gonads in the intestinal region.

Sub-tribus I. *Archireptantia*.

Without a snout. Central rhynchocoelomic diverticula. Small dorsal ganglia and a primitive cerebral organ. Different parts of stomodaeum sharply separated and well developed. Nephridia with a large, distal efferent duct. Without metameric vascular loops.

Sub-tribus II. *Eureptantia*.

With a snout. Peripheral rhynchocoelomic diverticula. Cerebral organs with a sac. Large, free dorsal ganglia. Different parts of stomodaeum continued into each other. Nephridia with, as a rule, proximal efferent ducts. With metameric vascular loops.

LEYDEN,

March 1, 1923.

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